Bivalve traits and distributions to explore species diversity at tropical and temperate tidal flats

Compton, Tanja Joan

Chapter 2.

Thermal tolerance ranges and climate variability: a comparison between bivalves from differing climates

Tanya J. Compton, Micha J.A. Rijkenberg, Jan Drent, Theunis Piersma

Journal of Experimental Marine Biology and Ecology 352 (2007) 200–211

Abstract

The climate variability hypothesis proposes that in variable temperate climates poikilothermic animals have wide thermal tolerance windows, whereas in constant tropical climates they have small thermal tolerance windows. In this study we quantified and compared the upper and lower lethal thermal tolerance limits of numerous bivalve species from a tropical (Roebuck Bay, north western Australia) and a temperate (Wadden Sea, north western Europe) tidal flat. Species from tropical Roebuck Bay had higher upper and lower lethal thermal limits than species from the temperate Wadden Sea, and Wadden Sea species showed an ability to survive freezing temperatures. The increased freezing resistance of the Wadden Sea species resulted in thermal tolerance windows that were on average 7°C greater than the Roebuck Bay species. Furthermore, at a local-scale, the upper lethal thermal limits of the Wadden Sea species were positively related to submersion time and thus to encountered temperature variation, but this was not the case for the Roebuck Bay species. A review of previous studies, at a global scale, showed that upper lethal thermal limits of tropical species are closer to maximum habitat temperatures than the upper lethal thermal limits of temperate species, suggesting that temperate species are better adapted to temperature variation. In this study, we show for the first time, at both local and global scales, that the lethal thermal limits of bivalves support the climate variability effect in the marine environment.

1. Introduction

The greater magnitude of temperature variation at temperate latitudes is expected to select for wider physiological tolerance windows in poikilothermic animals, whereas the smaller magnitude of temperature variation at tropical latitudes is expected to lead to narrower tolerance windows (Dobzhansky 1950, Stevens 1989). The relationship between climate variation and thermal tolerance windows has been termed the *climate variability hypothesis* (Stevens 1989). It has far-reaching implications for geographical range sizes and species richness patterns (Gaston et al. 1998).

Direct evidence for the climate variability hypothesis in the marine environment is scarce (Gaston et al. 1998, Spicer & Gaston 1999). The reason for a lack of support for the climate variability hypothesis, especially in the marine environment, is that few studies have examined the lower lethal thermal limits of organisms (Spicer & Gaston 1999). Thus, the effects of thermal acclimation on both heat and cold tolerance have seldomly been reported in multiple species adapted to different thermal habitats (Pörtner et al. 2006, Osovitz & Hofmann 2007). A large scale approach of examining physiological traits, macrophysiology (Chown et al. 2004), has proven promising in insects, and is expected to be an important for understanding species' distributions in the marine environment (Osovitz & Hofmann 2007). For example, a meta-analysis of the thermal limits of insects has shown that the lower rather than the upper lethal thermal limits of insects are correlated with latitude (Addo-Bediako et al. 2000, Sinclair et al. 2003).

Based on available knowledge, tolerance windows in marine organisms as estimated by lethal and critical thermal limits have displayed a relationship with climate regime. Note that lethal thermal limits can be used as indirect relevant correlates to examine biogeographical limits (Pörtner 2002). Fishes and bivalves from the Antarctic are known to have narrow thermal tolerance windows relative to temperate fishes with broad thermal tolerance windows that reflect the higher variation in their environmental temperatures (Somero & de Vries 1967, Brett 1970, Peck & Conway 2000, Peck et al. 2002). An adaptation to climate regime has also been shown in the upper lethal thermal limits of crabs and bivalves, as tropical species displayed higher upper lethal thermal limits than temperate species (Vernberg & Tashian 1959, Stillman & Somero 2000). In addition, where lower lethal thermal limits have been estimated in crabs it appears that tropical species have higher lower lethal thermal limits than temperate species (Vernberg & Tashian 1959). Interestingly, an examination of the upper thermal limits of porcelain crabs (Genus *Petrolisthes*) along the Pacific coast indicated that temperate species have a larger safety buffer in their upper thermal limits than temperate species (Stillman & Somero 2000, Stillman 2002).

To investigate whether congeneric bivalve species from intertidal sedimentary habitats display evidence of a climate variability effect, we measured lethal thermal limits of 18 bivalve species from a tropical (Roebuck Bay, North West Australia) and a temperate tidal flat (Wadden Sea, The Netherlands) in relation to the local climate regime at each location. Thermal tolerance windows were compared between bivalves from both locations to test for a climate variability effect. Seasonal acclimatisation was examined to observe whether differences between locations would be greater than seasonal differences. The upper lethal thermal limits were related to the local habitat to examine relationships with submergence time. To examine whether at a global scale bivalves display a relationship between their upper lethal thermal limits and habitat temperature we obtained additional values from the literature and examined this correlation.

2. Materials and methods

2.1. Local temperature variation

Annual climate regimes of the Roebuck Bay, North Western Australia (17°S and 122°E) and the Wadden Sea, The Netherlands (53°N and 5°E) tidal flats were recorded using Stowaway Tidbit™ loggers (hourly readings, buried 5 cm deep into the sediment) for periods of 6 to 12 months over a four year period (2002 to 2006). We averaged daily measurements to show seasonal trends in temperature, including yearly maxima and minima. The annual temperature range at each location was determined by subtracting the upper from the lower quartile value for each year.

2.2. Collection of bivalve species

The species sampled in this experiment represent all the numerically important species (Piersma et al. 2001, Pearson et al. 2003). At both locations most species were sampled at the tidal flat and one species was collected from a hard substrate (*Mytilus edulis* in Wadden Sea and *Barbatia pistachia* in Roebuck Bay). In The Netherlands one species was collected in the subtidal North Sea, *Spisula subtruncata* (although this species does appear in the intertidal occasionally, T.P. pers obs.). Overall, the thermal limits of eleven species in Roebuck Bay, and seven species in the Wadden Sea were determined. Bivalve species were collected directly before placement into the experiment, and thus the field temperature at the time of collection is regarded as the acclimatization temperature for each trial. All collection and handling of animals was completed according to the legal requirements of each country.

2.3 Experimental trials

The tested range of temperatures was 0 - 45°C for the bivalves from Roebuck Bay and -10 to 40°C for bivalves from the Wadden Sea; in both cases treatments were separated by 5°C intervals. All lethal thermal tolerance ranges were determined in the local sea-water. Each experiment tested only one species at a time. Each species' experiment was terminated at 24 hours, and at the end of the experiment a gaping response indicated death; i.e. the lack of adductor muscle contractions (Ansell et al. 1980a). In aquatic organisms, lethal limits are determined in the time-frame when survival is passive and time-limited at high temperatures, i.e. at the end-point of survival. During passive survival blood oxygen levels are minimal and life is supported by anaerobic metabolism, heat shock proteins and an antioxidative defence (Pörtner & Knust 2007).

Seasonal variation in the upper lethal thermal limits was examined for six of the 11 species in Roebuck Bay and five of the seven species in the Wadden Sea. Replicate species' trials within a season were completed for all species, except for *Gafrarium dispar* and *Mya arenaria*. In Roebuck Bay the winter species trials ran from July to August (2003), and the

summer species trials ran in November (2003). In the Wadden Sea the winter trials ran from February to March (2003), and the spring species trials ran in May (2003). In Roebuck Bay, the lower lethal thermal limits of all species were determined in November 2003. In the Wadden Sea species the lower temperatures from 20°C to -5°C were examined in May 2003, and as no species died, we tested another level of freezing tolerance (-10°C) in June 2004. Freezing tolerance limits were tested in spring due to logistical reasons.

Replicate (n=2) temperature treatment basins were used for both the warm (20- 45 °C) and cool (15 – 0 °C) temperature treatments. Within each basin salt water filled aquaria (n=3-6, size: 11.5 x 18 x 18 cm, WS salinity 28‰, RB salinity 35‰) held the experimental species at the desired temperature. Temperatures above 20°C were maintained in basins with aquarium heaters (Tetra™ (20°C, 25°C), Reptistat™ (35°C, 40°C) and Schlego™ heaters (40°C, 45°C)). In Roebuck Bay, temperatures below 20°C were maintained in basins that were held in air-conditioned rooms (20°C, 15°C), Engel™ refrigerator units (10°C, 5°C) and ice (0°C). For the Wadden Sea species, cool temperature basins were maintained in a climate room (15°C), a temperature controlled water bath using anti-freeze (MGW Lauda K2R) (10°C, 5°C) , basins with ice (0°C) and a temperature controlled cabinet (Weiss Enet Model HETK 3057.S, The Netherlands) (-5°C, -10°C). In the temperature treatment of -5 °C, aquaria filled with sea water were placed directly into the refrigerator unit. Temperature readings were taken every four hours. As temperatures varied by 1- 2°C, the average temperature from each basin, during an experimental trial, was used in the final analysis.

2.4 Phylogenetic analysis

Related species can share similar adaptations such that species can no longer be regarded as independent samples (Felsenstein 1985). To establish whether such effects of evolutionary history should be of concern, we examined whether the lethal thermal limits at both sites were related to phylogeny. In this study the phylogenetic topology of the bivalve species was drawn from Giribet and Wheeler (see Fig. 11, p 296, in Giribet & Wheeler 2002) and family descriptions from Beesley et al. (1998). To examine whether the bivalve thermal limits were phylogenetically constrained (Harvey & Pagel 1991), a test for serial independence was run (Abouheif 1999, Reeve & Abouheif 2003). In each simulation the relationship between lethal thermal limits and phylogeny was non-significant: upper lethal thermal limits $P = 0.48$, lower lethal thermal limits $P = 0.36$, lethal thermal range $P = 0.38$. Therefore, as the lethal thermal limits were not significantly correlated with phylogeny, traditional statistical analyses can be safely applied (Abouheif 1999, Ackerly & Reich 1999).

2.5 Tidal height and upper thermal limits

Submergence time was calculated from the two spatial mapping databases available for each location (see Pepping et al. 1999, Piersma et al. 2001). Based on the positive

occurrence of species in the spatial mapping database we calculated an average submergence time (hours) for each species. The average submergence time was then converted into a percentage (12.42 h is a full tidal cycle). Average submergence time (%) was estimated for all species, except for the two hard substrate species.

2.6 Statistical analyses

As mortality is a sigmoid function of temperature, a logit linear regression was used to separately estimate the upper and lower thermal limit of each species trial (day n=2, season n=2), and each replicate within a trial (basin n=2). The coefficients of the logit linear regression were used to calculate the temperature at which half of the sample population died within 24 h. All lethal thermal limit values are presented as a mean and standard error in the results.

Upper lethal thermal limits were tested separately for each species using a two-way ANOVA to examine differences between season and replicate species' trials. In species where season was not tested, a one-way ANOVA was used to examine differences between replicate species' trials. A summary of these statistical results are presented in Table 1. To determine whether the upper and lower lethal thermal limits are correlated, we ran a Pearson correlation. The lethal thermal tolerance windows (upper – lower thermal limits) of all the species were calculated and tested for a difference between the two locations in a one-way ANOVA. All statistical analyses were performed in the statistical package Systat® version 11.

3. Results

The temperature data demonstrated that the tidal flat temperatures at Roebuck Bay showed less annual variation (5.64 ± 2.05°C, mean ± SD of difference between upper and lower quartile) than the Wadden Sea (9.74 ± 2.11°C, mean ± SD of difference between upper and lower quartile) (Fig. 1). The Roebuck Bay tidal flat also attained higher maximum (32.51 ± 0.17°C, mean ± SE) and minimum (18.82 ± 0.75°C, mean ± SE) average daily temperatures relative to the Wadden Sea tidal flat (22 ± 1.14°C maximum and 1.89 ± 0.59°C minimum, mean ± SE).

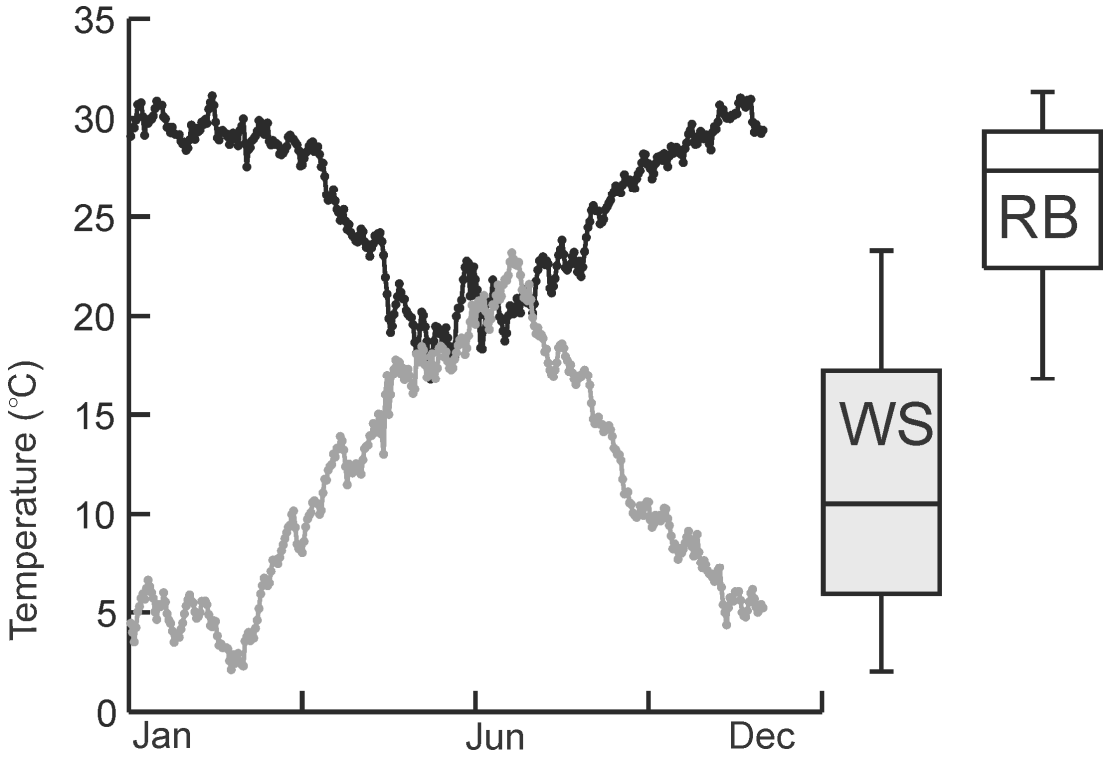

Figure 1. Annual and daily temperature variation at a tropical and temperate tidal flat. The dots represent the average daily temperature at each location. The black line represents Roebuck Bay (RB) and the grey line represents the Wadden Sea (WS). June temperatures are winter in Roebuck Bay and summer in the Wadden Sea. The boxplots show the annual temperature range. A boxplot shows 50% of the measured values, with the whiskers representing the outliers. The line in the middle of the boxplot represents the median value.

The average lethal thermal tolerance windows of the Roebuck Bay bivalve species were significantly narrower ($F_{1,56}$ = 42.29, P<0.01, 32.25 ± 0.52°C) than the four Wadden Sea species (38.52 ± 0.78°C, Fig 2). Furthermore, consistent with the field temperatures, the Roebuck Bay species displayed both higher average upper (37.11 ± 0.33°C) and higher average lower lethal thermal limits (4.98 ± 0.32°C, Fig. 2), than the Wadden Sea species whose average upper lethal thermal limits were 29.80 ± 0.42°C and average lower lethal thermal limits were -7.07 ± 1.14°C. Thus, the Roebuck Bay bivalves can survive about 5°C above their average maximum habitat temperatures, whereas the Wadden Sea species can survive by about 7°C above their average maximum habitat temperatures. The lower lethal thermal limits of the Roebuck Bay bivalves were about 14°C below their average minimum field temperatures, and the Wadden Sea bivalves survived about 9°C below their minimum field temperatures. In the Wadden Sea species there was also a tendency for the average

upper and lower lethal thermal limits to be positively correlated ($P = 0.10$, Fig. 3), with no trend in the Roebuck Bay species ($P = 0.93$).

In the Wadden Sea tidal flat, the average field temperature in February was approximately 4°C and in May was approximately 14°C (Fig 1). These seasonal differences in field temperature are, however, not reflected by a change in the upper lethal thermal limits of the Wadden Sea bivalves ($P \geq 0.05$ in Table 1). Only *Macoma balthica* showed a slight increase of 1.5°C in temperature tolerance from winter to spring ($F_{1,5} = 15.62$, $P = 0.01$ in Table 1). Within the sediment of the Roebuck Bay tidal flat, the average field temperature in June was approximately 19°C and in November was approximately 29°C. The upper lethal thermal limits of the Roebuck Bay bivalve species, however, did not show a response to an increase in seasonal temperature ($P \geq 0.05$ in all cases, Table 1). Furthermore, the statistical effect of replicate species' trial was mainly not significant at both locations ($P \geq 0.05$ in most cases, Table 1), as only three out of 16 species showed a significant difference. This suggests that the experimental results are robust.

Within the Roebuck Bay tidal flat, the bivalves showed no significant relationship between their upper lethal thermal limits and average submergence time ($r = -0.38$, $n = 10$, $P = 0.28$, Fig. 4). However, in the Wadden Sea tidal flat the bivalves did show a significant negative relationship between upper lethal thermal limits and average submergence time ($r = -0.88$, $n = 6$, $P = 0.02$) (Fig. 4). In the Wadden Sea, the two high intertidal species (*Cerastoderma edule* and *Abra tenuis*) showed higher upper thermal limits than the predominantly low intertidal and subtidal species (*Tellina tenuis* and *Spisula subtruncata*) (Fig. 4). In addition, the hard substrate species (*Mytilus edulis*) in the Wadden Sea displayed a significantly reduced upper lethal thermal limit relative to the other tidal flat species (excluding the subtidal North Sea *S. subtruncata*, $F_{1,34} = 7.69$, $P < 0.01$) (Table 1). In contrast, the hard substrate species at Roebuck Bay (*Barbatia pistachia*) did not have a significantly reduced upper lethal thermal limit ($F_{1,66} = 0.33$, $P = 0.57$) compared to the temperate species (*M. edulis*).

Table 1. Lethal thermal limit values of the Roebuck Bay and Wadden Sea species. The mean upper and lower lethal thermal limits (including standard error (SE)) are shown. The one- and two-way ANOVA's results for differences between replicate species' trials (S.T.) and seasons are included (degrees of freedom (DF), F-value and P-value). No data is indicated by a slash (-). The replicate trials are indicated by n. The lethal thermal tolerance range and the average submergence (subm.) time are included for each species. Authority names from McMillan (1968) and from Lamprell & Whitehead (1992).

	Upper thermal tolerance (C)								Lower thermal tolerance (C)								Range	submergence
	Season	Mean	S.E.	DF	Fvalue	p(day)	Fvalue	p(season)	n	Season	Mean	S.E.	DF	Fvalue	p(day)	n		time (%)
Roebuck Bay species																		
Anadara granosa	summer	41.45	1.31	2,3	330.39	0.00			6	4.82	1.31	0.01	1,2	142.20	0.01	4	36.63	21.97
Barbatia pistachia	summer	36.22	0.53	1,5	0.043	0.85	0.99	0.37	8	6.01	0.81	0.07	1,2	13.21	0.07	4	30.21	
	winter	36.87	0.29															
Anadontia bullula	summer	36.31	0.81	1,2	9.56	0.09			4	7.17	1.65	0.62	1,2	0.33	0.62	4	29.14	39.87
Divericella irpex	summer	36.94	0.51	1,2	2.42	0.26			4	5.51	0.52	0.93	1,2	0.01	0.93	4	31.43	39.38
Anomalocardia squamosa	summer	37.30	0.42	1,5	0.63	0.81	0.45	0.53	8	3.05	0.73	0.37	1,2	1.35	0.37	4	34.25	25.63
	winter	37.76	0.45															
Gafrarium dispar	summer	41.76	1.44						2	7.32	0.49					2	34.44	17.14
Siliqua sp.	summer	33.45	0.80	1,5	5.75	0.06	1.23	0.32	8	6.14	0.40	0.31	1,2	1.81	0.31	4	27.31	40.64
	winter	31.99	1.57															
Tellina capsoides	summer	37.97	0.85	1,5	2.35	0.19	0.13	0.74	8	3.35	0.24	0.00	1,2	9147.56	0.00	4	34.61	17.09
	winter	38.25	0.21															
Tellina piratica	summer	37.58	0.10	1,5	0.69	0.44	0.28	0.62	8	3.63	0.87	0.03	1,2	37.97	0.03	4	33.95	34.54
	winter	37.42	0.28															
Tellina sp. (oval)	summer	36.31	0.81	1,5	0.24	0.65	0.42	0.54	8	3.52	0.95	0.12	1,2	7.00	0.12	4	32.80	11.17
	winter	35.75	0.08															
Corbula sp.	summer	37.722	0.92	1,2	59.50	0.02			4	5.46	0.60	0.95	1,2	0.01	0.95	4	32.26	58.97

Table 1. Continues

Wadden Sea species																	
Mytilus edulis	winter	28.34	0.11	1,5	0.41	0.55	1.02	0.36	8	-13.40	1.49	0.09	1,2	10.20	0.09	4	41.73	
	summer	27.41	0.87															
Cerastoderma edule	winter	32.19	0.63	1,5	0.10	0.77	3.23	0.13	8	-6.18	0.34	0.48	1,2	0.74	0.48	4	38.38	60.03
	summer	33.98	0.67															
Spisula subtruncata	winter	26.97	0.64	1,5	0.95	0.38	0.09	0.78	8									100.00
	summer	26.60	1.07															
Mya arenaria	winter	30.46	0.20	1,2			2.91	0.23	4									62.27
	summer	31.32	0.47															
Abra tenuis	winter	33.44	0.73	1,2	0.00	0.99			4	-1.68	0.07	0.88	1,2	0.03	0.88	4	35.12	45.03
Macoma balthica	winter	29.43	0.39	1,5	1.89	0.23	15.62	0.01	8	-7.01	0.61	0.44	1,2	0.92	0.44	4	36.45	65.69
	summer	30.97	0.14															
Tellina tenuis	winter	27.57	0.50	1,2	109.35	0.01			4									72.37

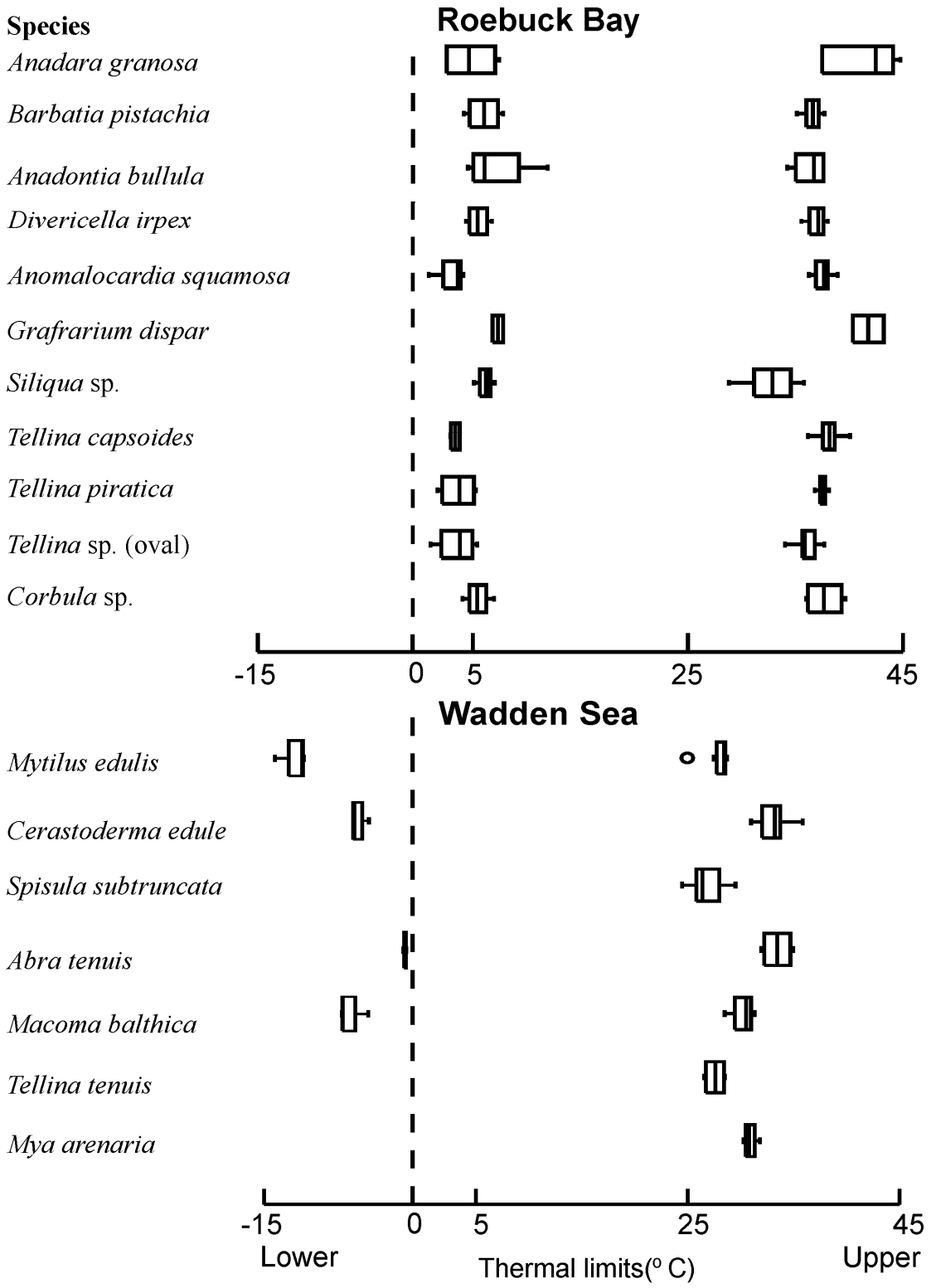

Figure 2. Upper and lower lethal thermal limits of bivalve species from Roebuck Bay and the Wadden Sea. The boxplot of each species represents the range of basin, day and season estimates. The stippled line represents the 0°C value. A boxplot displays the median, the upper and lower quartile.

4. Discussion

In agreement with the climate variability hypothesis, the temperate species from the Wadden Sea tidal flat had lethal thermal tolerance windows approximately 7°C greater than those of the tropical Roebuck Bay species that appeared to reflect the greater temperature variation measured in the temperate sediments. This shows that the Wadden Sea species can survive across a wider range of temperatures before they cease to function. The tropical Roebuck Bay species displayed an ability to survive higher temperatures in their upper lethal thermal limits than the temperate species, whereas the temperate Wadden Sea species survived cooler temperatures than the tropical species. These results are consistent with studies on crabs Decapoda.

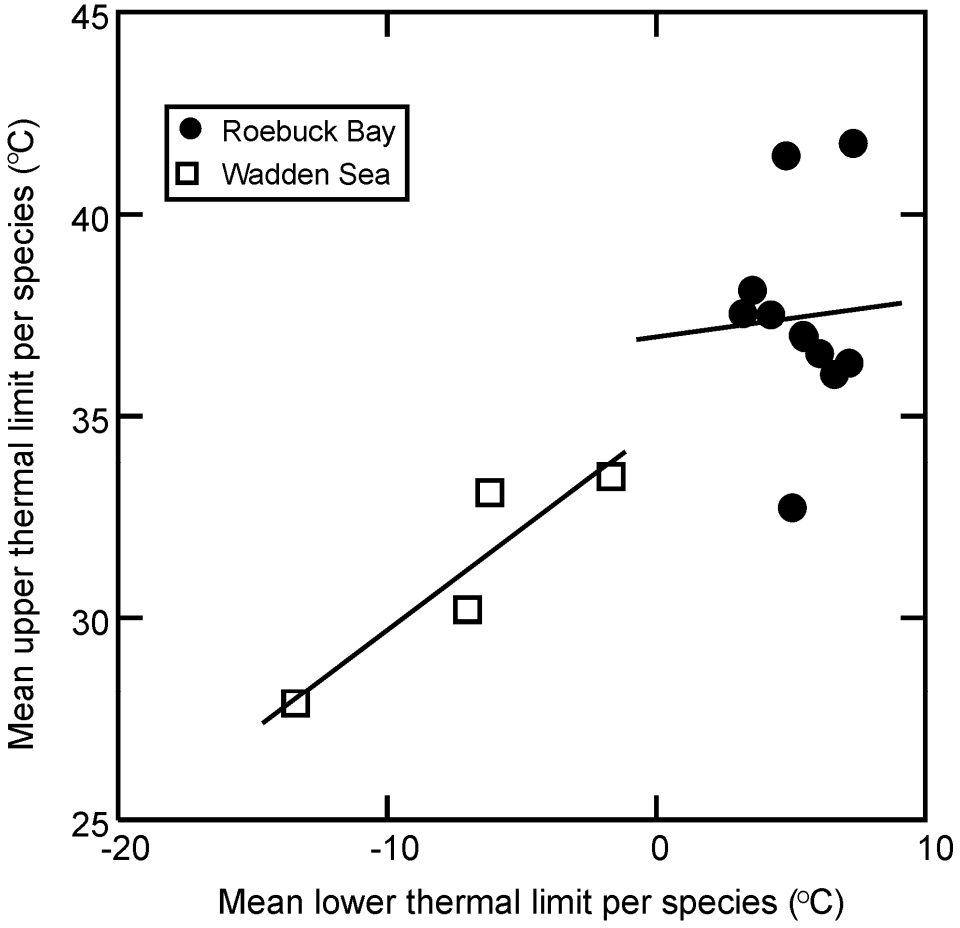

Figure 3. The relationship between the upper and lower lethal thermal limits at each location. In Roebuck Bay there is no correlation between the mean upper and lower lethal thermal limits, whereas in the Wadden Sea a correlation is apparent but not significant.

Tropical fiddler crabs (*Uca*) could not survive cool temperatures (Vernberg & Tashian 1959), and tropical crabs from the Genus *Uca* and *Petrolisthes* had higher upper lethal

thermal limits than temperate crabs (Vernberg & Tashian 1959, Stillman & Somero 2000, Stillman 2002).

In the temperate Wadden Sea the local tidal flat temperatures dropped markedly from summer to winter, and concurrent with this observation, the species showed a remarkable ability to survive freezing temperatures. Freezing resistance has also been reported in other molluscs (Peck & Conway 2000, Davenport & Davenport 2005). Although the exact cause of death as the result of freezing is still debated, cell damage due to either or both changes in osmotic gradients and ice-crystal damage are considered most likely (Loomis 1995). In insects, lower lethal thermal limits show the most dramatic change with latitude (Addo-Bediako et al. 2000, Sinclair et al. 2003). Whether lower lethal thermal limits display the greatest change with latitude in marine invertebrates is unknown. However, our results indicate that the lower lethal thermal limits display greater differences between the tropical and temperate species than the upper lethal thermal limits. In marine invertebrates it is expected that freeze tolerance enabled range expansion into colder waters (Aarset 1982).

Seasonal acclimatization differences were not apparent in the upper and lower lethal thermal limits of most species at both locations. The lack of a seasonal effect is not necessarily surprising, as previously established seasonal changes in bivalve lethal thermal limits were generally small, only a 1 – 2°C change in lethal thermal limits with an increase of 10-15°C in water temperature (Ansell et al. 1980a, 1980b). Furthermore, interspecific differences in upper lethal thermal limits have been shown to be greater than acclimation-induced effects in porcelain crabs (Stillman & Somero 2000). Although acclimation of lethal limits was very limited, this does not exclude the importance of thermal acclimation for physiological processes in the normal "operating temperature ranges".

Like Davenport and Davenport (2005) for rocky intertidal molluscs, we found that the upper and lower lethal thermal limits of the Wadden Sea species were positively correlated, with a 10% likelihood that the correlation represents a chance event. A positive correlation between the upper and lower lethal thermal limits might suggest a trade-off in the physiological mechanisms needed to deal with upper and lower thermal limits (Pörtner 2002). A trade-off suggests that in adapting to new environments and acquiring new characters or greater performance, organisms sometimes experience a correlated decline in other structures or functions (Pörtner et al. 2006).

At a local-scale the average upper lethal thermal limits and submergence time were negatively correlated in the Wadden Sea, and thus to encountered temperature variation. This result is in agreement with other studies from buffered sandy substrates that have only studied one to three bivalve species across a tidal gradient (Ansell et al. 1980a, 1980b). In porcelain crabs (*Petrolisthes*), upper lethal thermal limits were related to tidal height, and are expected to have evolved in response to microhabitat temperatures as they were not related to phylogeny (Stillman & Somero 2000,

Stillman 2002). This suggests that at a local scale lethal thermal limits in bivalves can predict local distributions. Interestingly, recent evidence has shown that temperatures within the 'normal' performance range of an organism are also important for understanding species' distributions. For example, a small rise in temperature just outside the 'normal operating temperature range' of an organism, rather than heat-induced death per se, can result in a lowered scope for growth and reproduction (Pörtner & Knust 2007, Wang & Overgaard 2007).

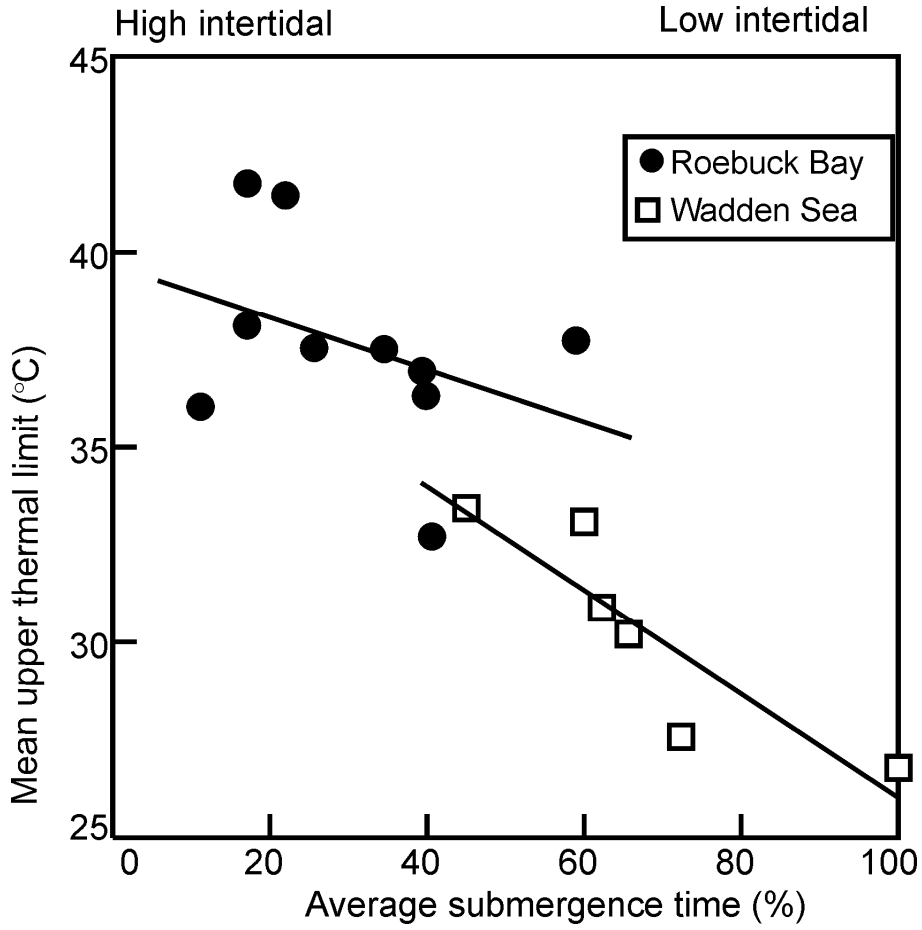

Figure 4. The relationship between the upper lethal thermal limits of each species and submergence time (%). The upper lethal thermal limits of the Wadden Sea species are correlated with submergence time, whereas the upper lethal thermal limits of the Roebuck Bay species are not.

The lack of a negative correlation between upper lethal thermal limits and submergence time in Roebuck Bay might be due to the species' occurrences over a more limited range of higher intertidal areas than the Wadden Sea species. Alternatively, the larger range of sediment and habitat types at Roebuck Bay (Pepping et al. 1999) might provide a wider variety of microhabitats that enable lower body temperatures to be maintained at higher tidal elevations (Helmuth 2002), i.e. species

at high intertidal levels do not experience more temperature variation than low intertidal species.

The upper lethal thermal limit of *Mytilus edulis*, from the Dutch Wadden Sea, showed a significantly lower upper lethal thermal limit relative to the other species at this location. This is surprising as it could be expected that a rocky intertidal species would have higher upper lethal thermal limits, than sedimentary tidal flat species, which are buffered by a layer of sediment and interstitial water. One explanation for a lower upper lethal thermal limit in *M. edulis*, relative to the tidal flat species, is that this species usually lives as a cluster of bivalves attached together by byssal threads. Living as a cluster protects this species from temperature extremes (Helmuth 1998). In contrast to *M. edulis*, a lower lethal thermal limit is not displayed in the rocky intertidal species (*Barbatia pistachia*) from Roebuck Bay that lives in clusters within rock crevices. These contradicting results might suggest that upper lethal thermal limits are dependent on the microhabitat of an individual species (Helmuth 2002).

Results from our study suggested that the tropical species live closer to their maximum habitat temperature (~ 4.6°C) than the temperate species (~ 7.8°C). To examine whether this trend was general at a global scale, we compiled data from the literature, and compared the upper lethal thermal limits in relation to the maximum habitat temperature of bivalve species from sites in the northern and southern hemisphere, using an analysis of covariance (Fig. 5, Appendix 1). The upper lethal thermal limits of bivalves were correlated with maximum habitat temperature ($F_{1,47}$ = 12.87, $P < 0.01$), and exceeded maximum temperatures by an average of 7.12 ± 0.52°C, in all but two (*Donax semistriatus* (G) and *Siliqua* sp. (J)) cases. There was no difference in the regression slopes of the northern and southern hemisphere species ($F_{1,46}$ = 2.38, $P = 0.13$). Most strikingly, the species inhabiting higher temperatures live closer to their maximum habitat temperatures (t-value 4.33, $P<0.01$). In crabs upper thermal limits were also closer to maximum habitat temperatures at tropical sites than temperate sites (Stillman & Somero 2000, Stillman 2002).

The observed relationship between upper lethal thermal limits and habitat temperatures at both global and local habitat scales, in this study, tally well with the suggestions of Stillman and associates (Stillman & Somero 2000, Stillman 2002). Stillman et al. suggested that there are physiological costs involved in maintaining higher thermal tolerance limits, and that temperate species maintain a broader capacity to survive changes in temperature. Furthermore, it can be expected that differing thermal window widths in various climates are associated with physiological costs (Pörtner et al. 2006).

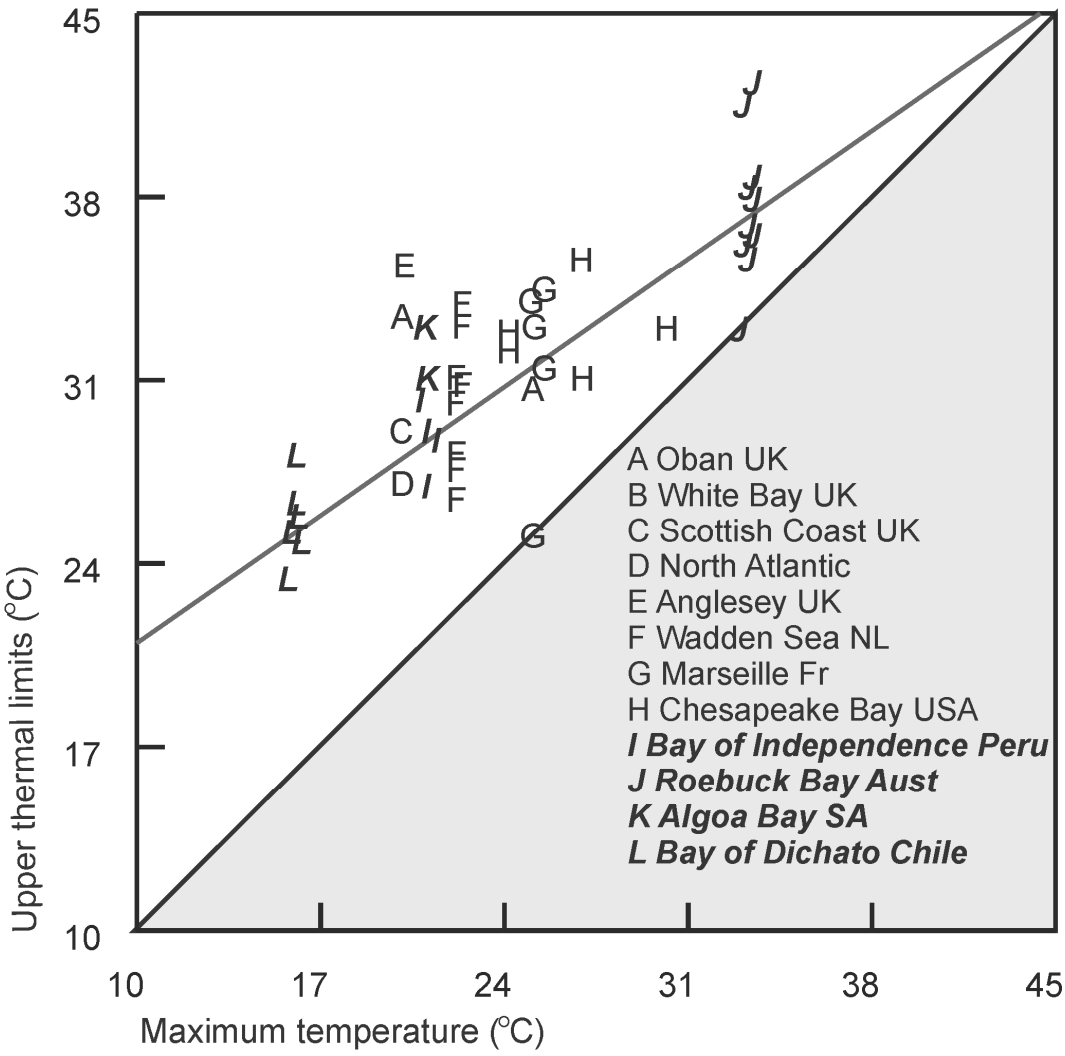

Figure 5. The relationship between the upper lethal thermal limits and the maximum habitat temperature of bivalves from a number of sites shows a difference between warmer and colder living bivalves. As the regression slope of the bivalve upper lethal thermal limits is significantly different from 1 (i.e. the grey shaded area), this indicates that species inhabiting warmer temperatures live closer to their maximal habitat temperatures than temperate species. The basic data are presented in Appendix 1.

The thermal tolerance windows of bivalves, as estimated by lethal thermal limits, are consistent with the climate variability hypothesis; revived by Stevens (1989). To quantify thermal limits at a global-scale, future studies might increase the geographic range of study, and determine whether differently defined thermal limits, i.e. pejus temperatures, show a similar or stronger response to geographical location (Pörtner 2002, Osovitz & Hofmann 2007). Finally, our finding of narrower lethal thermal tolerance ranges in tropical species places the suggestion that tropical areas act as source habitats for bivalve speciation and range expansion towards temperate and high-latitude zones (Jablonski et al. 2006) in an interesting light. On the basis of

our results only, we would predict temperate species to have a higher chance to invade tropical areas rather than the reverse.

Acknowledgements

We are grateful for the use of the facilities at the Broome TAFE Aquaculture Centre, W.A. Fisheries, the DEC office in Broome and the Broome Bird Observatory. For help in the field we thank C. Abma, K. Krans, R. de Jonge, R. Kentie, H. Sombroek and G. Morton. We owe many thanks to G. B. Pearson for logistical support and W. J. Wolff for all kinds of help, including comments on this manuscript. We are also grateful to F. Vézina and an anonymous reviewer for useful comments on the manuscript. Identifications of species were completed by M. Lavaleye and R. Willan. TJC is funded by an Ubbo Emmius scholarship from the University of Groningen.

References

Aarset AV (1982) Freezing tolerance in intertidal invertebrates (a review). Comp Biochem Physiol 73A:571-580

Abouheif E (1999) A method for testing the assumption of phylogenetic independence in comparative data. Evol Ecol Res 1:895-909

Ackerly DD, Reich PB (1999) Convergence and correlations among leaf size and function in seed plants: A comparative test using independent contrasts. Am J Bot 86:1272-1281

Addo-Bediako A, Chown SL, Gaston KJ (2000) Thermal tolerance, climatic variability and latitude. Proc Royal Soc B 267:739-745

Ansell AD, Barnett PRO, Bodoy A, Masse H (1980a) Upper temperature tolerances of some European molluscs. 1. *Tellina fabula* and *T. tenuis*. Mar Biol 58:33-39

Ansell AD, Barnett PRO, Bodoy A, Masse H (1980b) Upper temperature tolerances of some European molluscs. 2. *Donax vittatus*, *D. semistriatus* and *D. trunculus*. Mar Biol 58:41-46

Beesley PL, Ross GJB, Wells A (1998) Mollusca: The Southern Synthesis, Vol Part A xvi 563 pp. Part B. viii 565 -1234 pp. CSIRO publishing, Melbourne

Brett JR (1970) Fish: functional approaches. In: Kinne O (ed) Marine Ecology, Vol 1, Environmental Factors, Part 1, Chapter 3: *temperature*. Wiley-Interscience, Chichester, p 515-616

Chown SL, Gaston KJ, Robinson D (2004) Macrophysiology: large-scale patterns in physiological traits and their ecological implications. Funct Ecol 18:159-167

Davenport J, Davenport J (2005) Effects of shore height, wave exposure and geographical distance on thermal niche width of intertidal fauna. Mar Ecol Prog Ser 292:41-50

Dobzhansky T (1950) Evolution in the tropics. Amer Sci 38:209-221

Felsenstein J (1985) Phylogenies and the comparative method. Am Nat 125:1-15

Gaston KJ, Blackburn TM, Spicer JI (1998) Rapoport's rule: time for an epitaph? Trends Ecol Evol 13:70-74

Giribet G, Wheeler W (2002) On bivalve phylogeny: a high-level analysis of the Bivalvia (Mollusca) based on combined morphology and DNA sequence data. Invertebr Biol 121:271-324

Harvey PH, Pagel MD (1991) The comparative method in evolutionary biology, Oxford University Press

Helmuth BST (1998) Intertidal mussel microclimates: Predicting the body temperature of a sessile invertebrate. Ecol Monogr 68:51-74

Helmuth BST (2002) How do we measure the environment? Linking intertidal thermal physiology and ecology through biophysics. Integr Comp Biol 42:837-845

Jablonski D, Roy K, Valentine JW (2006) Out of the tropics: Evolutionary dynamics of the latitudinal diversity gradient. Science 314:102-106

Lamprell K, Whitehead T (1992) Bivalves of Australia, Vol 1. Crawford House Press, Bathurst

Loomis SH (1995) Freezing tolerance of marine invertebrates. Oceanog Mar Biol, Ann Rev 33:337 - 350

McMillan NF (1968) British Shells, Vol. William Clowes and Sons, Limited, London

Osovitz CJ, Hofmann GE (2007) Marine macrophysiology: studying physiological variation across large spatial scales in marine systems. Comp Bioch Physiol A 147:821 - 827

Pearson GB, Piersma T, Lavaleye M, de Goeij P, Honkoop P, Rogers D, Hickey R, Slack-Smith S (2003) Life in Land's edge-birds of Roebuck Bay 2002. LANDCOPE Expedition Report 48. Report No. ISSN 1444-8742, Department of Conservation and Land Management, Perth, Western Australia

Peck LS, Conway LZ (2000) The myth of metabolic cold adaptation: oxygen consumption in stenothermal Antarctic bivalves. In: Harper E, Crame AJ (eds) Evolutionary Biology of the Bivalvia. Special Publications177, Geology Society, London, p 441-450

Peck LS, Portner HO, Hardewig I (2002) Metabolic demand, oxygen supply, and critical temperatures in the antarctic bivalve *Laternula elliptica*. Physiol Biochem Zool 75:123-133

Pepping M, Piersma T, Pearson GB, Lavaleye M (1999) Intertidal sediments and benthic animals of Roebuck Bay, Western Australia., NIOZ-report 1999-3, The Netherlands

Piersma T, Koolhaas A, Dekinga A, Beukema JJ, Dekker R, Essink K (2001) Long-term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden Sea. J Appl Ecol 38:976-990

Pörtner HO (2002) Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. Comp Bioch Physiol A 132:739-761

Pörtner HO, Bennett AF, Bozinovic F, Clarke A, Lardies MA, Lucassen M, Pelster B, Schiemer F, Stillman JH (2006) Trade-offs in thermal adaptation: The need for a molecular to ecological integration. Physiol Biochem Zool 79:295-313

Pörtner HO, Knust R (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. Science 315:95-97

Reeve J, Abouheif E (2003) Phylogenetic Independence. Department of Ecology and Evolution, SUNY at Stony Brook

Sinclair BJ, Vernon P, Klok CJ, Chown SL (2003) Insects at low temperatures: an ecological perspective. Trends Ecol Evol 18:257-262

Somero GN, de Vries AL (1967) Temperature tolerance of some Antarctic fishes. Science 156:257-258

Spicer JI, Gaston KJ (1999) Physiological diversity and its ecological implications, Blackwell Science., Oxford, UK

Stevens GC (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. Am Nat 133:240-256

Stillman JH (2002) Causes and consequences of thermal tolerance limits in rocky intertidal porcelain crabs, genus *Petrolisthes*. Integ Comp Biol 42:790-796

Stillman JH, Somero GN (2000) A comparative analysis of the upper thermal tolerance limits of Eastern Pacific Porcelain crabs, Genus *Petrolisthes*: Influences of latitude, vertical zonation, acclimation and phylogeny. Physiol Biochem Zool 73:200-208

Vernberg FJ, Tashian RE (1959) Studies on the physiological variation between tropical and temperate fiddler crabs of the genus *Uca*.1. Thermal death limits. Ecology 40:589-593

Wang T, Overgaard J (2007) The heartbreak of adapting to global warming. Science 315:49-50